

Contribution to the Knowledge of the Genus *Atholus* (Coleoptera: Histeridae: Histerinae: Histerini) from the Indonesian Archipelago

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(Received 29 June 2023; Accepted 25 February 2024)

Some of the Indonesian species of the genus *Atholus* Thomson, 1859 are re-examined based on museum specimens. *Atholus famulus* (Lewis, 1892), *A. myrmidon* (Marseul, 1861) and *A. singalanus* (Marseul, 1880) are re-described, and SEM micrographs and illustrations of available genitalia are provided. Additional Indonesian records of *A. bifrons* (Marseul, 1854), *A. coelestis* (Marseul, 1857), *A. philippinensis* (Marseul, 1854) and *A. torquatus* (Marseul, 1854) are reported. A key to the Indonesian species is provided.

Key Words: redescription, SEM, new records, taxonomy, identification key.

Introduction

The complex biogeographical system and history of the Indonesian archipelago creates either wide dispersal of fauna among the islands, or high restriction to limited areas (Lohman et al. 2011). Over the past 50 million years, the geography of this region has changed considerably, and various events have made way to generate remarkable patterns in the distribution of its insect fauna, and its diversification. This might also have the same effect with terrestrial beetles, particularly in members of the family Histeridae, which likely expanded their range from the continental Asia towards the Greater Sunda Islands when the Sunda Shelf still existed during the Pleistocene (Bird et al. 2005). The rising and falling of sea levels during this epoch led these islands to repeatedly split and fuse, potentially causing the confinement of several taxa to certain islands (Lohman et al. 2011). In addition, the Wallace Line may also play a vital role in establishing the faunal boundary for histerid beetles between the Sunda Shelf to the east and Wallacea and its oceanic islands to the west.

The genus *Atholus* Thomson, 1859 includes to date 78 species and one subspecies (Bickhardt 1917; Mazur 2011, 2013), with an almost cosmopolitan distribution with the exception of continental Australia and Antarctica. All species are characterized by a fairly small size, oval and generally black and shining hard exoskeleton, and they occur in

a wide variety of decaying matters, especially plant debris and ruminant dung. The knowledge of Oriental species has been established and updated by the contributions of several histerologists over the last 170 years (e.g., Marseul 1854, 1857, 1861, 1862, 1870, 1873, 1880; Lewis 1889, 1892, 1899, 1900, 1901, 1902, 1908, 1915; Schmidt 1889, 1897; Bedel 1906; Bickhardt 1914a, b; Desbordes 1925; Reichardt 1932; Ôhara 1999; Mazur 2013; dela Cruz and Ôhara 2022, 2023a, b; Ho et al. 2023). Thirteen species are currently reported from the Indonesian archipelago (Mazur 2011), mainly from the Greater Sunda Islands (i.e., Borneo, Java, Sulawesi and Sumatra). However, most of the original descriptions of the Indonesian taxa (Marseul 1854, 1857, 1861, 1880; Lewis 1889, 1892, 1899, 1900, 1902; Schmidt 1897) are inadequately characterized needing redescription, even revision. Hence, in the present paper *A. famulus* (Lewis, 1892), *A. myrmidon* (Marseul, 1861) and *A. singalanus* (Marseul, 1880) are re-described, providing supplemental figures and illustrations. In addition, new collecting localities in the Greater Sunda Islands and new records from the islands of Lesser Sunda (Bali, Sumbawa and Sumba), are reported for *A. bifrons* (Marseul, 1854), *A. coelestis* (Marseul, 1857), *A. philippinensis* (Marseul, 1854), and *A. torquatus* (Marseul, 1854). These additions are primarily based on collections made by the authors, except for the first one.

This paper also provides a remark on the taxonomic status of *Atholus mundulus* (Lewis, 1902) as a valid, or at least considered as a dubious species to date, contrary on its cur-

rent taxonomic placement as a synonym with *A. genuae* (Lewis, 1888), or with *A. torquatus* (Mazur 1984).

Materials and Methods

All examined specimens are housed in the Insect Collection of the Systematic Entomology, Hokkaido University Museum (SEHU) and Insect Collection at the Museum Zoologicum Bogoriense (MZB). Dissections have been carried out under stereo microscopes (Nikon SMZ800 and Nikon SMZ745T with Nikon Digital Sight DS-Fi2), while micrographs of external morphology were taken using SEM microscope (JEOL JSM-6510). Genitalia were treated in 10% KOH at 60°C for an hour, washed in 80% ethyl alcohol, soaked in acid fuchsin at 60°C for 3 hours, re-treated in a glacial acetic acid and methyl salicylate (1:1) mixture for 15 minutes, washed in xylene for 15 seconds, and observed in α -terpineol. Species descriptions also include measurements of body length and width following Ôhara (1994), namely: PEL (length between anterior angles of pronotum and apices of elytra), APW (width between anterior angles of pronotum), PPW (width between posterior angles of pronotum), EL (length of elytron along sutural line) and EW (maximal width between outer margins of elytra).

Systematics

Genus *Atholus* Thomson, 1859

Atholus Thomson, 1859: 76 [type species: *Hister bimaculatus* Linnaeus, 1758 (p. 358), originally designated]; Schmidt 1885: 288; Ganglbauer 1889: 369; Lewis 1906: 402; Bickhardt 1917: 159, 162; Bickhardt 1919: 13, 137, 139; Auzat 1924: 93; Arnett 1962: 378, 381; Halstead 1963: 7, 8; Witzgall 1971: 179, 183; Kryzhanovskij and Reichardt 1976: 382; Mazur 1984: 210; Ôhara 1992: 167–182; Ôhara 1993: 135–148.

Peranus Lewis, 1906: 401 [type species: *Hister scutellaris* Erichson, 1834 (p. 151); synonymized by Kryzhanovskij and Reichardt (1976: 384)].

Atholister Reitter, 1909: 286 [type species: *Hister scutellaris* Erichson, 1834 (p. 151); synonymized by Heyden (1910: 317)].

Euatholus Kryzhanovskij in Kryzhanovskij and Reichardt, 1976: 387 [type species: *Hister duodecimstriatus* Schrank, 1781 (p. 39); synonymized by Mazur (1984: 210)].

Key to the Indonesian Species of the Genus *Atholus* (Modified from Desbordes 1917), Excluding *A. mundulus*

1. Lateral pronotal striae two
..... *A. tenuistriatus* (Lewis, 1889)
- Lateral pronotal stria one 2
2. Apical end of third dorsal stria strongly bent inwards

- *A. coelestis* (Marseul, 1857)
- Third dorsal stria of elytra not bent inwardly 3
3. Lateral pronotal stria complete, continued as anterior stria behind the head. 4
- Lateral pronotal stria interrupted in the anterolateral angle 8
4. Elytral dorsal striae 1–3 entire, dorsal stria 4 present only on apical end 5
- Elytral dorsal striae 1–4 complete 6
5. External subhumeral stria of elytra long, slightly abbreviated on apical fourth
..... *A. philippinensis* (Marseul, 1854)
- External subhumeral stria of elytra short, reduced to an arc, present on basal end.
..... *A. singalanus* (Marseul, 1880)
6. Pygidium strongly punctate
..... *A. bifrons* (Marseul, 1854)
- Pygidium smooth or finely punctate 7
7. External subhumeral stria of elytra very short or absent; prosternal lobe punctate
..... *A. terraemotus* (Lewis, 1900)
- External subhumeral stria of elytra well-marked on medio-basal portion; prosternal lobe smooth.
..... *A. myrmidon* (Marseul, 1861)
8. Pronotal foveae behind anterolateral angle present ...
..... *A. tetricus* (Lewis, 1902)
- Anterolateral area of pronotum without foveae 9
9. Propygidium with shallow excavation with coarse punctures inside, occupying middle and a little more than the posterior half *A. gestroi* (Schmidt, 1897)
- Propygidium normal, with no conspicuous excavation on the surface. 10
10. Apex of lateral pronotal stria arched behind the anterior angle. 11
- Apex of lateral stria of pronotum not arched behind the anterior angle 12
11. Lateral stria of pronotum more shortened basally and less hamate on the apical end; pygidium smooth
..... *A. pinnulae* (Lewis, 1900)
- Lateral stria of pronotum less shortened basally and more hamate on the apical end; punctures in pygidium becoming finer apically. ... *A. torquatus* (Marseul, 1854)
12. Anterior margin of clypeus with strong indentation, the anterior edge before the eye deeply notched; pygidium with irregular and sparse punctures
..... *A. crenatifrons* (Lewis, 1899)
- Anterior margin of clypeus normal, feebly sinuous laterally; pygidium entirely smooth
..... *A. famulus* (Lewis, 1892)

Atholus bifrons (Marseul, 1854)
(Figs 1A, 11D)

Hister bifrons Marseul, 1854: 545 (type locality: India).

Atholus bifrons: Lewis 1906: 402 (listed); Mazur 1984: 211; Mazur 1997: 129 (India, Indonesia: Sumatra, Vietnam, Thailand, Hongkong); Mazur 2008: 90; Mazur 2009: 113; Mazur 2011: 103 (additional records: Taiwan; cata-

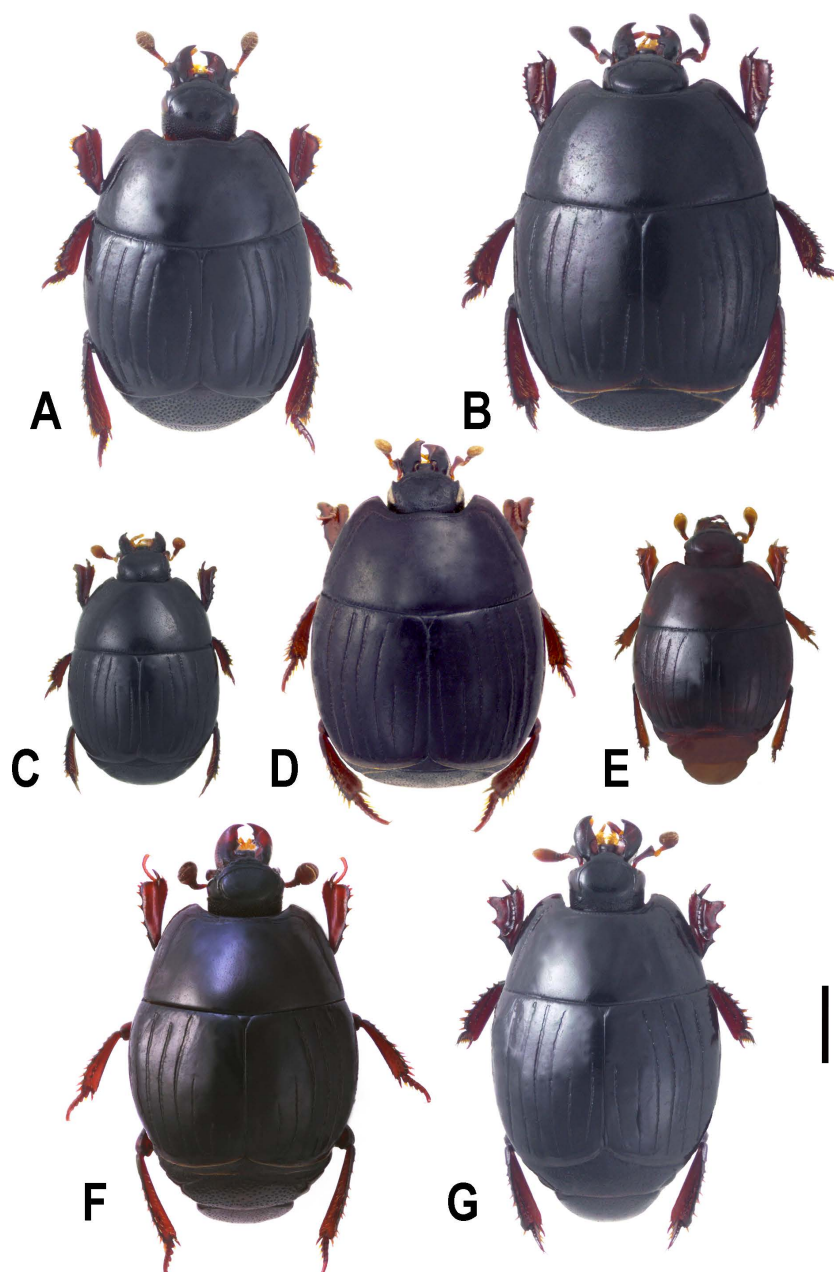


Fig. 1. Some Indonesian *Atholus*, dorsal habitus. A, *Atholus bifrons* (Marseul, 1854), IC-22-in01; B, *A. philippinensis* (Marseul, 1854), IC-22-in06; C, *A. coelestis* (Marseul, 1857), IC-22-in02; D, *A. myrmidon* (Marseul, 1861), IC-22-in05; E, *A. famulus* (Lewis, 1892), IC-22-in03; F, *A. singalanus* (Marseul, 1880), IC-22-in07; G, *A. torquatus* (Marseul, 1854), IC-22-in08. Scale bar: 1.00 mm.

logued); dela Cruz and Ôhara 2022: 237–245 (Japan: Ryukyus, Indonesia: Borneo; SEM, male and female genitalia).

Hister (Atholus) bifrons: Bickhardt 1910: 53; Bickhardt 1917: 193 (catalogued); Desbordes 1917: 323 (keyed).

Specimens examined. Two♂♂, 2♀♀, and 2 specimens of undetermined sex. **Sumatra Island:** Central Sumatra, Payakumbuh, Harau Valley, March to September 1993, Sarimundanas leg. (1♀ SEHU, 1♀ MZB). **Borneo Island:** West Kalimantan, Mt. Bawang, 250–300 m a.s.l., October 1990, unknown collector [IC-22-id01] (1♂ and 1 ex. SEHU, 1♂ and 1 ex. MZB).

Diagnosis. *Atholus bifrons* can be recognized by the fore-

head divided into two by rather weak median longitudinal impression and remarkable punctations of both propygidium and pygidium.

Distribution. India, Thailand, Vietnam, China: Hong Kong, Taiwan, Ryukyu islands of Japan, and Indonesia: Sumatra and Borneo Islands (Fig. 11D).

Remark. The Indonesian distribution of this species previously recorded only from Sumatra has been recently extended to Borneo (dela Cruz and Ôhara 2022).

Atholus coelestis (Marseul, 1857)
(Figs 1C, 11A)

Hister coelestis Marseul, 1857: 416, pl. 10, fig. 59 (type local-

ity: China).

Hister femoralis Motschulsky, 1863: 449 [synonymized by Lewis (1885: 465)].

Atholus coelestis: Lewis 1906: 402 (listed); Lewis 1915: 55 (Formosa); Mazur 1984: 212; Ôhara 1992: 173–176 (Nansei islands; redescription, male genitalia); Mazur 1997: 129; Ôhara 1999: 31–32; Mazur 2011: 104 (Oriental region, Tajikistan, Comores; catalogued); Mazur et al. 2015: 1454; Ho et al. 2023: 41–42 (Taiwan); dela Cruz and Ôhara 2023a: 1–26 (Philippines); dela Cruz and Ôhara 2023b: 13–38 (Japan).

Hister (Atholus) coelestis: Bickhardt 1910: 53 (catalogued); Bickhardt 1917: 193 (catalogued); Desbordes 1917: 320 (keyed); Desbordes 1919: 399 (Tonkin, Annam, Cochinchine); Desbordes 1921: 10 (Inde); Kamiya and Takagi 1938: 31 (listed).

Atholus (Euatholus) coelestis: Hisamatsu and Kusui 1984: 17 (noted, key).

Atholus (Euatholus) coelestes [sic]: Hisamatsu 1985: 228, pl. 41, fig. 61 (noted, keyed, imaged).

Specimens examined. Seventy-one specimens of undetermined sex. **Sumatra Island:** Central Sumatra, Payakumbuh, Harau Valley, November 1993, Sarimudanas leg. (2 exs SEHU, 1 ex. MZB). **Java Island:** West Java, Sukabumi, Jampang, Tgl., 9712001, Bojong Pari, 21–22 December 1997, alt. 640 m, E. and E. Cholik leg. (3 exs MZB); W. Java, 18. 3000, 20.30, Localitij, W. Preanger, November 1941, Groenendael leg. (1 ex. MZB); W. Java, Bandoeng, 24 January 1940, 700 m, J. Olthof leg. (1 ex. MZB); Java, Preanger, N.O.I., Bandoeng, 25 February 1936, alt. 750 m, F. C. Drescher leg. (1 ex. MZB); Java, Preanger N.O.I., Bandoeng, 12 February and 8 March 1936, alt. 750 m, F. C. Drescher leg. (4 exs MZB); Preanger, Bandoeng, 17 May 1932, F. C. Drescher leg. (1 ex. MZB); Tjijatj. [= Tjilatjap], August 1925, unknown collector (1 ex. MZB). **Borneo Island:** Kalimantan Timur, Kab. Kutai Kartanegara, 01.03042°S, 116.56526°E, Ds. Karya Merdeka RT09, Kec. Samboja, 18 November 2007, M. Ôhara leg. [KL-07-MO-028] (1 ex. SEHU). **Sulawesi Island:** Zuld Celebes, Nanggala, Rantepao, October 1937, alt. 900 m, F. C. Drescher (11 exs MZB); Nanggala, November 1937, unknown collector (4 exs MZB); Kabupaten Maros [near Makassar], 05.1008°S, 119.4038°E, 40 m. a.s.l., Cagar Alam Bantimurung, 27 October 2000, M. Ôhara leg. [SU-00-MO-002] (1 ex. SEHU, 1 ex. MZB); Kabupaten Barru, 04.2527°S, 119.3646°E, 2 m. a.s.l., Desa Tung, Kecamatan Barru, 28 October 2000, M. Ôhara leg. [SU-00-MO-005] (3 exs SEHU, 2 exs MZB); Kabupaten Tana Toraja, Kec. Makale, Tondon, 02.5744°S, 119.5442°E, 750 m. a.s.l., Pasar Hewan Bolu, Desa Bolu, Kecamatan Tallunglipu, 30 October 2000, M. Ôhara leg. [SU-00-MO-012] (1 ex. SEHU); Provinsi Sulawesi Selatan, Parepare, Mallusetasi, 04.0538°S, 119.3657°E, 3 m. a.s.l., Desa Bojo, Kecamatan Mallusetasi, 31 October 2000, M. Ôhara leg. [SU-00-MO-016] (3 exs SEHU, 2 exs MZB); Kab. Bolaang Mongondow, Kec. Dumoga Barat, 00.0118°N, 123.5633°E, Desa Doloduo, Kosingolan, 1 September 2006, M. Ôhara leg. [SU-06-MO-054] (1 ex. SEHU); Kab. Bolaang Mongondow, Dumoga Barat,

00.3947°N, 124.0636°E, Desa Bumbungan, Kec. Dumoga, 2 September 2006, M. Ôhara leg. [SU-06-MO-057] (2 exs SEHU, 2 exs MZB); Provinsi Sulawesi Utara, Kab. Bolaang Mongondow, 00.5913°N, 124.1401°E, Desa Nonapan, Kec. Poigar, 2 September 2006, M. Ôhara leg. [SU-06-MO-059] (1 ex. SEHU); Kab. Maros, Kec. Bantimurung, Ds. Bontebonte, 04.5541°S, 119.0702°E, 3 September 2006, M. Ôhara leg. [SU-06-MO-063] (1 ex. SEHU); Kab. Maros, Kec. Simbang, Desa Samangki, 05.0243°S, 119.4243°E, 3 September 2006, M. Ôhara leg. [SU-06-MO-064] (1 ex. SEHU); Kab. Maros, Kec. Bantimurung, Desa Bantimurung, 05.0143°S, 119.4035°E, 3 September 2006, M. Ôhara leg. [SU-06-MO-065] (1 ex. SEHU); Sulawesi, Provinsi Sulawesi Selatan, Kab. Maros, Kec. Cenrana, Desa Limapocoe, 5 September 2006, G. Takaku leg. [SU-06-GT-069] (1 ex. SEHU, 1 ex. MZB); Provinsi Sulawesi Selatan, Kab. Maros, Kec. Cenrana, Ds. Lebbotengae, 5 September 2006, G. Takaku leg. [SU-06-GT-070] (1 ex. MZB); Sulawesi Selatan, Bantimurung, 27 December 1999, N. Ohbayashi leg. [IC-22-02] (2 exs SEHU, 1 ex. MZB). **Bali Island:** Sangeh, 10 February 1997, M. Kasagi leg. (1 ex. SEHU, 1 ex. MZB); 22 March 1981, K. Sugino leg. (1 ex. SEHU, 1 ex. MZB). **Sumbawa Island:** Provinsi Nusa Tenggara Barat, Kabupaten Sumbawa Besar, Ropang, 08.5044°S, 117.1722°E, Hutan Malaka Desa Malaka, 9 November 2000, M. Ôhara leg. [SB-00-MO-033] (2 exs SEHU, 1 ex. MZB); Kabupaten Bima, Belo, 08.3713°S, 118.4324°E, Desa Ngali, Kecamatan Belo, 12 November 2000, M. Ôhara leg. [SB-00-MO-041] (2 exs SEHU, 1 ex. MZB). **Sumba Island:** Provinsi Nusa Tenggara Timur, Kabupaten Sumba Timur, Kota Waingapu, 09.4055°S, 120.1219°E, Kecamatan Kota Waingapu, Kambajawa, 30 January 2003, M. Ôhara leg. [SM-03-MO-020] (1 ex. SEHU).

Diagnosis. *Atholus coelestis* is characterized by its third dorsal stria extending inwardly towards the apical end of the fourth and fifth striae. Sometimes, the apex of the fourth stria also extends slightly towards the fifth stria. Among all the Indonesian *Atholus*, *A. coelestis* is discriminated for its slight emargination on its anterior margin of mesoventrite.

Distribution. China, Indochina, Sri Lanka, Nepal, Tajikistan, Comoros, Japan, Taiwan, Philippines, Indonesia: Greater Sunda (Sumatra, Java, Borneo and Sulawesi Islands), Lesser Sunda (Bali, Sumbawa and Sumba Islands) (Fig. 11A).

Remark. The slight emargination of on the anterior margin of its mesoventrite is unique to *A. coelestis* among all the Oriental and East Palearctic *Atholus*.

Atholus crenatifrons (Lewis, 1899)

(Fig. 12)

Hister crenatifrons Lewis, 1899: 17 (type locality: Sumatra).

Atholus crenatifrons: Lewis 1906: 402 (listed); Mazur 1984: 212; Mazur 1997: 130; Mazur 2011: 104 (catalogued).

Hister (Atholus) crenatifrons: Bickhardt 1910: 54; Bickhardt 1917: 193 (catalogued); Desbordes 1917: 322 (keyed).

Specimens examined. No specimen available for this study.

Diagnosis. *Atholus crenatifrons* is described as possessing a deep notch above the antennal insertions on its anterior edge margin of the head. The lateral stria of its pronotum is straight and non-hamate on the apical tip. The external sub-humeral stria of this species is almost complete, abbreviated shortly on both apical and basal ends. Also, the pygidia of *A. crenatifrons* is irregular, and not closely nor coarsely punctured.

Distribution. Indonesia: endemic to Sumatra Island (Fig. 12).

***Atholus famulus* (Lewis, 1892)**
(Figs 1E, 2A–F, 3A–H, 4A–F, 5A–C, 12)

Hister famulus Lewis, 1892: 346 (type locality: Sumatra).

Atholus famulus: Lewis 1906: 402; Mazur 1984: 214; Mazur 1997: 131; Mazur 2011: 105 (catalogued).

Hister (Atholus) famulus: Bickhardt 1910: 54; Bickhardt 1917: 194 (catalogued); Desbordes 1917: 319 (keyed).

Hister sp.: Aoki and Harada 1982: 346, 369.

Specimens examined. One ♂ and 1 ♀. **Borneo Island:** 1 km north of Camp Pemantus, 73 km north of Sotek, alt. 310 m, natural forest, East Kalimantan, 23 December 1980,

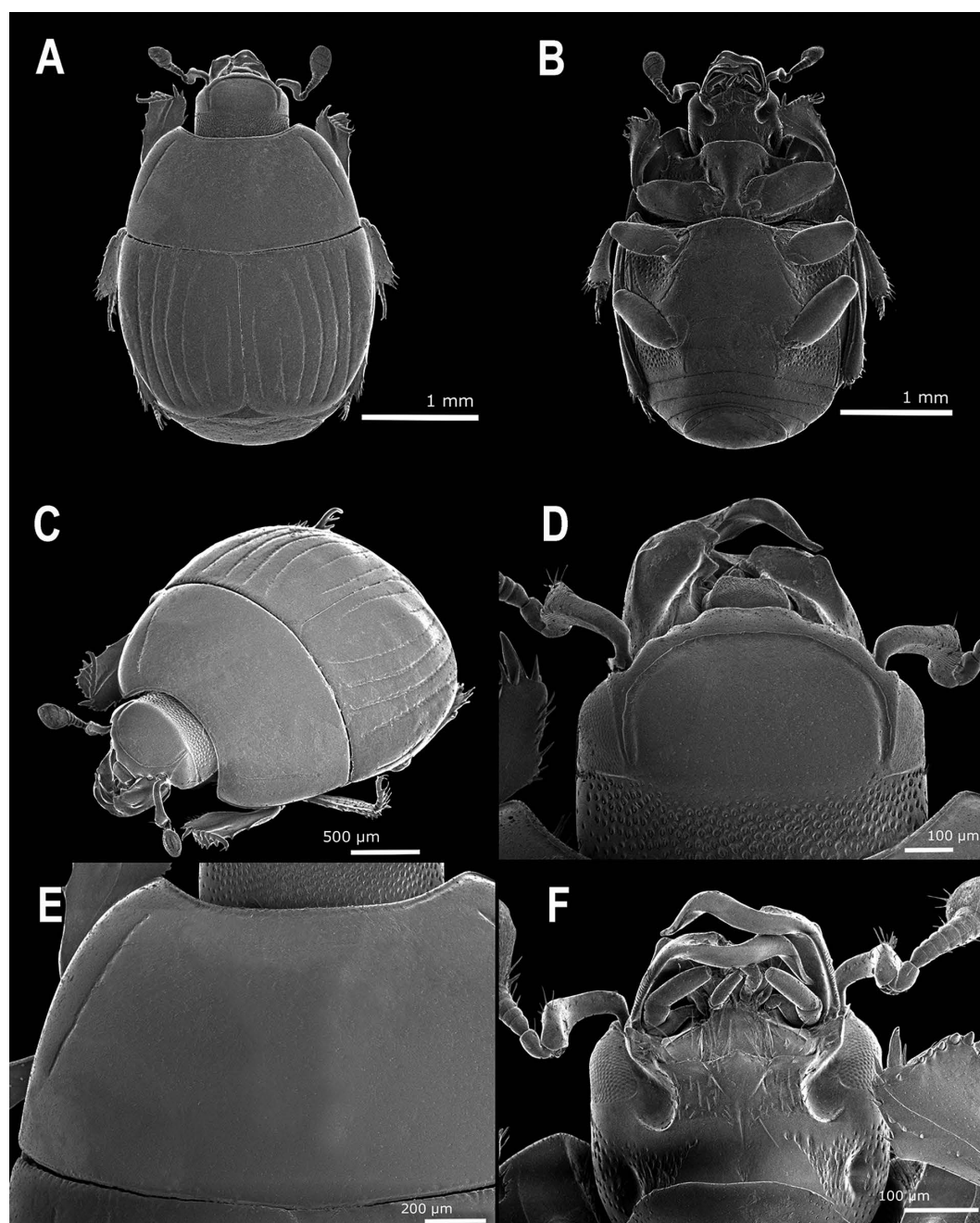


Fig. 2. *Atholus famulus* (Lewis, 1892), SEM micrographs, IC-22-in03. A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, dorsal view; E, pronotum; F, mouthparts, ventral view.

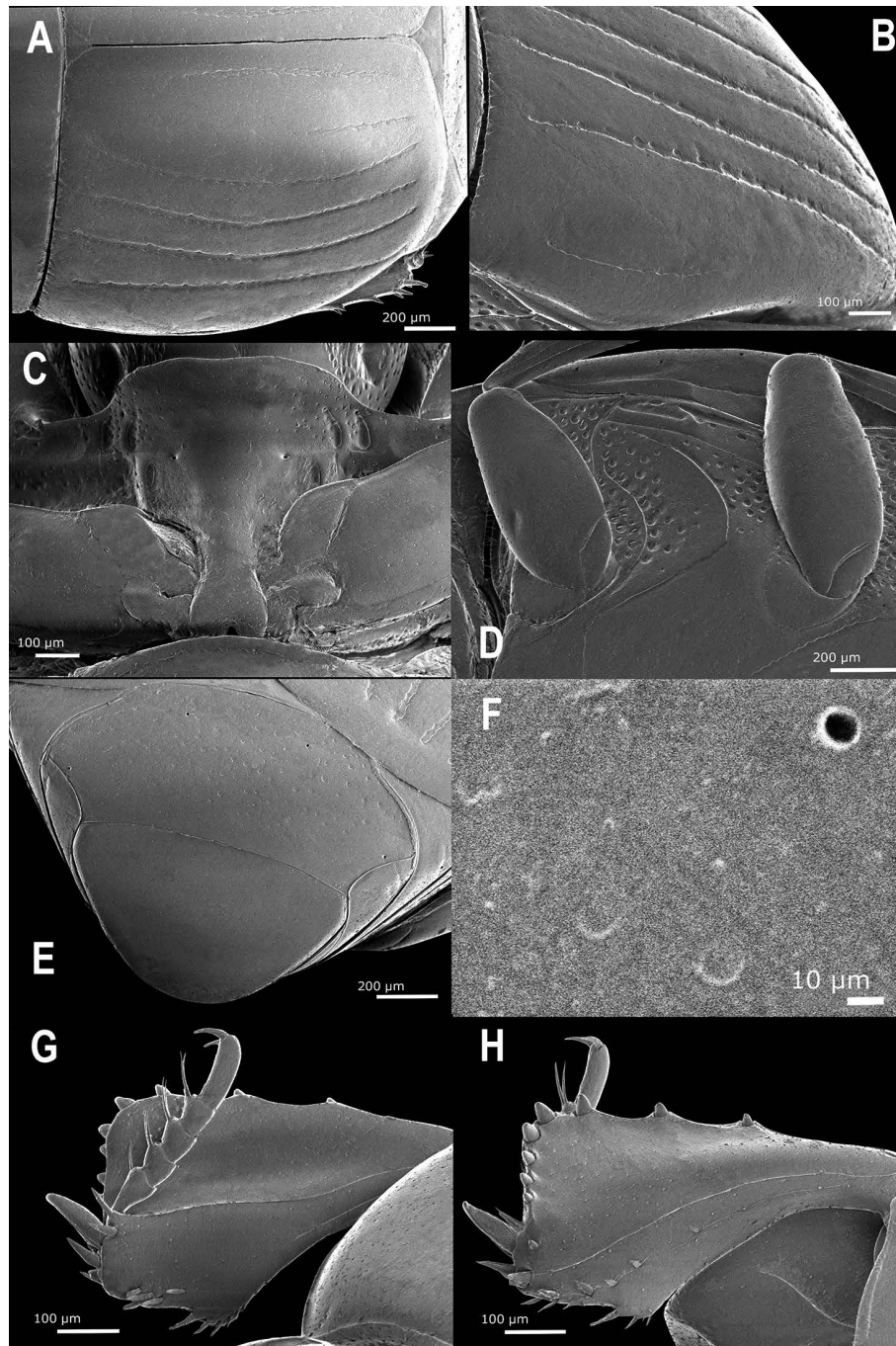


Fig. 3. *Atholus famulus* (Lewis, 1892), SEM micrographs, IC-22-in03. A, Elytra, dorsal view; B, ditto, oblique view; C, prosternal process; D, meso- and metaventrite; E, propygidium and pygidium; F, propygidium (punctuation); G, protibia, dorsal view; H, ditto, ventral view.

J. Aoki leg. (Bo-14A) [IC-22-in03, IC-22-in04]; (1♂ and 1♀ SEHU) (Aoki and Harada 1982).

Diagnosis. *Atholus famulus* is remarkable for its strongly dilated protibia, which is almost trilobed-like in structure. The male aedeagus is also quite peculiar having a small extended membrane on its anterior portion, but inconspicuous.

Re-description. Male, female. Body length: PEL: 3.00, 3.25 mm; APW: 1.25, 1.25 mm; PPW: 2.44, 2.60 mm; EL: 1.70, 1.70 mm; EW: 2.75, 2.80 mm. Body (Figs 1E, 2A–C) oval and convex; color from dark rufous to black; tibia, antenna, mouthparts and apical elytral margin rufous.

Head. Apical margin of clypeus entire, anterolateral margin feebly sinuous laterally; frontal stria (Fig. 2D) round and deeply impressed; disk covered sparsely with fine punctures, separated by five times their diameter, with alutaceous ground sculpture; occipital fovea absent; eyes well-visible dorsally; labrum strigate on surface, slightly oblong, labral fringe absent; mandible rather small, outer margin rounded and curved inwardly, mandibular apex acutely pointed.

Pronotum. Marginal stria laterally complete, weak on anterolateral angle; lateral pronotal stria (Fig. 2E) short and deeply impressed, the lateral stria rather distant from the margin, its basal end abbreviated to basal 3rd, the apical

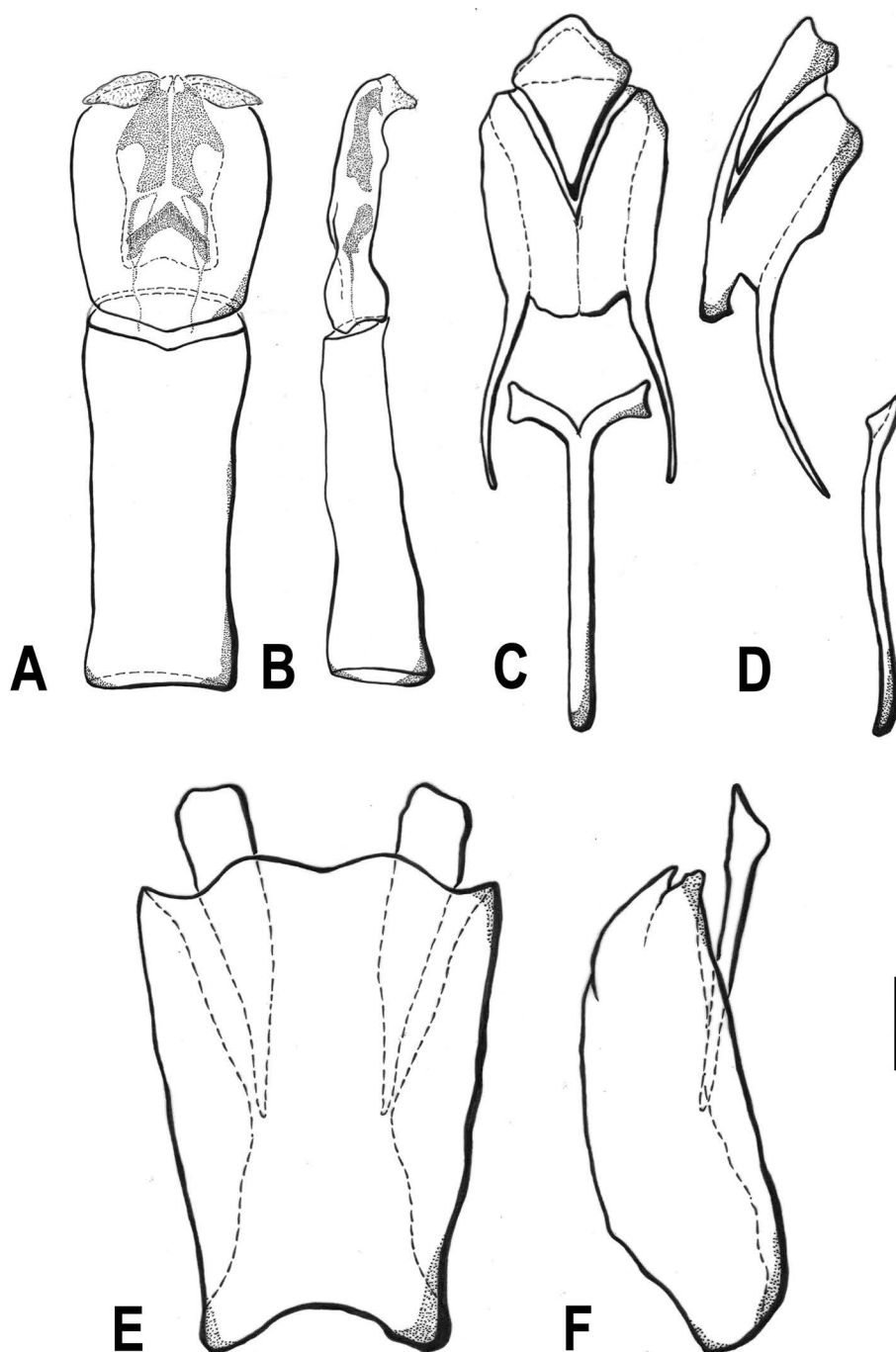


Fig. 4. *Atholus famulus* (Lewis, 1892), male genitalia, IC-22-in03. A, Aedeagus, dorsal view; B, ditto, lateral view; C, ninth and tenth tergites, and spiculum gastrale, dorsal view; D, ditto, lateral view; E, eighth tergite and sternite, dorsal view; F, ditto, lateral view. Scale bar: 0.20 mm.

end interrupted; anterior pronotal stria present, feebly connected to marginal stria; disk with sparse microscopic punctures, clothed with alutaceous microsculpture; area behind apical angle bare; posterior margin with very sparse, inconspicuous punctures; ante-scutellar region with short puncture.

Elytra. Anterior margin with row of short, longitudinal striae present on apical area around antero-scutellum; epipleural fossette bare; epipleural marginal stria absent; elytral marginal stria complete; external subhumeral (Fig. 3B) stria present medio-basally; internal subhumeral stria ab-

sent; oblique stria lightly impressed on basal third; dorsal striae (Fig. 3A) 1–4 complete, dorsal stria 5 present on apical third, sutural stria moderately longer, reaching beyond middle, abbreviated on basal third; disk surface similar to pronotum with alutaceous microsculpture.

Propygidium and pygidium. Propygidium (Fig. 3E, F) finely and loosely punctate, few shallow and coarse punctures scattered on basal area; pygidial (Fig. 3E) punctations similar to that of propygidium, becoming smooth on apex.

Prosternum. Prosternal lobe with moderately truncate and short anterior margin (Fig. 3C), medio-apical end as-

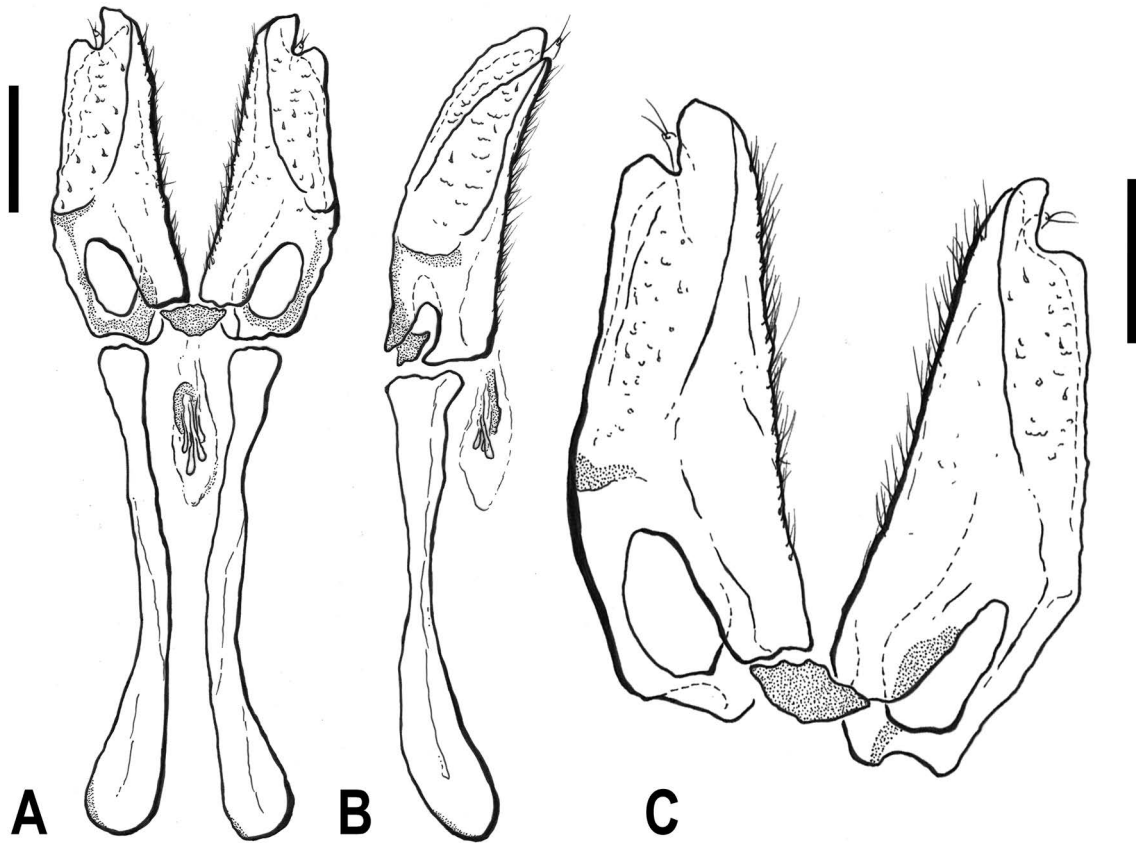


Fig. 5. *Atholus famulus* (Lewis, 1892), female genitalia, IC-22-in04. A, Dorsal view; B, lateral view; C, gonocoxite, dorsolateral view. Scale bars: 0.20 mm.

ending, marginal stria absent, striae present on basolateral ends brief and carinated; lobe with setiferous coarse punctures on anterolateral region, interspace among these punctures with sparse fine punctations, prosternal suture inconspicuous; prosternal process clothed with sparse fine punctures, the lateral sides descending; descending lateral stria moderately impressed and carinate; lateral disk with very few fine punctations; basal half of process narrow, posterior margin of basal lobe strongly emarginated.

Meso- and metaventrite. Anterior margin arcuate outwards (Fig. 3D), marginal stria complete, moderately impressed, stria behind anterolateral angle present; disk sparsely clothed with fine punctures on basal margin, which are separated by three to five times their diameter; meso-metaventral suture lightly impressed, complete and lightly angulated at middle; metaventral lateral (Fig. 3D) stria deeply impressed and carinated, extending obliquely and posteriorly, united with oblique stria which inwardly extends from basal third of metaventro-metepisternal suture; post-mesocoxal stria extending posteriorly and strongly curved along the posterior margin of mesocoxa, almost attaining the metaventro-mesepimeral suture; metaventrite with punctations of intercoxal disk similar to those of the apex of mesoventral plate; row of coarse punctures sometimes present along inside of basal portion of lateral stria; longitudinal suture lightly impressed; lateral disk of metaventrite densely covered with setiferous, large, round, shallow punctures; interspaces among the large punctures with

sparse, fine to coarse punctations; mesepimeron and metepimeron covered with densely setiferous, large punctures, interspaces among the punctures with few, fine to coarse punctations; metepisternum with sparse punctures on apical half; first abdominal sternite with punctation of intercoxal disk of similar to that of metaventrite; surface of lateral disk similar to mesepimeron and metepimeron; lateral stria deeply impressed, slightly carinate and complete.

Legs. Anterior surface of protibia (Fig. 3G) strongly dilated, becoming broader towards apical region, appearing trilobed; surface clothed with few, fine ocelloid punctures; the median area with weak strigate sculpture; outer lateral margin with three weak teeth topped with small denticles; anterior protibial stria complete and moderately impressed; inner marginal stria present almost on basal half; posterior surface (Fig. 3H) covered with sparse, fine punctures, the outer surface of ground sculpture strigate, the outer region slightly descending; number of denticles on both outer lateral margin and apical margin combined 9, one on inner apical angle; spur moderately long, almost half the length of protarsus; median posterior stria complete and moderately impressed; inner posterior stria lightly impressed with row of few sclerotized setae. Protarsal groove shallow. Protarsus with two spine-like tarsal denticles present; another one or two more distant, located at inner anterior angle; profemur sparsely clothed with fine punctations, the surface with strigate ground sculpture; marginal and anterior striae absent; femoral stria complete; posterior margin with few,

large punctations, row of setae present on apical end.

Male genitalia. Aedeagus (Fig. 4A, B) slightly stout, apically curved ventrad; parameres shorter, about half the length of phallobase; median lobe sclerotized; the anterior portion with extended membrane covered with sparse, short setae; eighth tergite (Fig. 4E, F) entire, with longitudinal fold on both lateral sides; ninth tergite (Fig. 4C, D) with lateral folds; tenth tergite simple; spiculum gastrale almost as same length as ninth tergite, bifurcate on apical fifth.

Female genitalia. Anterior portion of valvifers (Fig. 5A, B) paddle-shaped; gonocoxite (Fig. 5C) slightly elongate, almost as twice as broad, shovel-like; inner and outer surfaces differentiated; inner face moderately separated outer face by elevated lateral ridge; sclerotized setae on apical quarter of outer face short and slightly dense; inner face with short and sparse setae; apex of gonocoxite with two teeth; gonostyli present, articulated; spermathecae multiple, consisting of four sacs; sacs gradually enlarged and elongate, not sclerotized.

Distribution. Indonesia: Greater Sunda (Sumatra and Borneo Islands) (Fig. 12).

Remark. This species is relatively small, about the same body size of *A. coelestis*.

Atholus gestroi (Schmidt, 1897)
(Fig. 12)

Hister gestroi Schmidt, 1897: 293 (type locality: Sumatra).

Atholus gestroi: Lewis 1906: 402 (listed); Mazur 1984: 214; Mazur 1997: 131; Mazur 2011: 105 (Myanmar: Taninthari; catalogued).

Hister (Atholus) gestroi: Bickhardt 1910: 54; Bickhardt 1917: 194 (catalogued); Desbordes 1917: 324 (key).

Specimens examined. No specimen available for this study.

Diagnosis. *Atholus gestroi* is recognized by its remarkable transverse excavation on the medio-apical region of its propygidium. The shallow excavation is coarsely punctated, while the basal and lateral sides of propygidium are smooth. The lateral pronotal stria of this species is also abbreviated and is not connected to the anterior pronotal stria. The sub-humerus of elytra without any striae, and the protibial tooth on the apical end is prominent.

Distribution. Indonesia: Greater Sunda (Sumatra Island), Myanmar: Taninthari (Fig. 12).

Atholus mundulus (Lewis, 1902)
(Fig. 12)

Hister mundulus Lewis, 1902: 238 (type locality: Sumatra).

Hister (Hister) mundulus: Bickhardt 1910: 46 (catalogued).

Hister (Atholus) mundulus: Bickhardt 1917: 194 (catalogued); Desbordes 1919: 399 (listed with remarks).

Atholus mundulus: Mazur 1984: 218; Mazur 1997: 135; Mazur 2011: 106 [synonymized with *A. torquatus* based from Desbordes (1919)].

Specimens examined. No specimen available for this study.

Diagnosis. *Atholus mundulus* bears a complete and semi-circular frontal stria. The lateral stria of its pronotum is hamate on the apical end and ceasing in the anterolateral angle. The outer subhumeral stria is short medially, and dorsal striae 1–4 of elytra is complete. Dorsal elytral stria 5 on the apical half, a little beyond the middle, and the sutural stria abbreviated beyond the base. Both propygidium and pygidium are faintly punctulate. The marginal stria of prosternum is complete, while the protibia has three simple teeth.

Distribution. Indonesia: endemic to Sumatra Island (Fig. 12).

Notes. This species has been regarded as a synonym of *A. torquatus* on the basis of the Mazur's (1984) catalogue, who reports this synonymy as stated by Desbordes (1919). However, upon carefully verifying and interpreting Desbordes' remark, he reported *A. mundulus* as a valid species, even though he affirms: "... Par contre, je ne vois guère, dans les descriptions, de caractère bien net pour le distinguer de *H. (Atholus) genuae* Lew.; [now synonym of *Atholus torquatus*]; mais, ne connaissant pas l'espèce de Sumatra, je ne puis rien affirmer" [= ... On the other hand, I hardly see, in the descriptions, any very clear character to distinguish it from *H. (Atholus) genuae* Lew.; but, not knowing the species of Sumatra, I could not affirm anything]. In other words, Desbordes has not synonymized *A. mundulus* with *A. genuae*, much less with *A. torquatus*. Consequently, *A. mundulus* should be considered valid until the study of type specimen proves otherwise.

Atholus myrmidon (Marseul, 1861)
(Figs 1D, 6A–F, 7A–H, 8A–F, 12)

Hister myrmidon Marseul, 1861: 542 (type locality: Sulawesi).

Atholus myrmidon: Lewis 1906: 402 (listed); Mazur 1984: 215; Mazur 1997: 131; Mazur 2011: 105 (New Guinea, Laos; catalogued).

Hister (Atholus) myrmidon: Bickhardt 1910: 54; Bickhardt 1917: 194 (catalogued); Desbordes 1917: 324 (keyed).

Specimen examined. One ♂. **Sulawesi Island:** Propinsi Sulawesi Selatan, Kabupaten Maros, near Makassar, 05.0108°S, 119.4038°E, 40 m a.s.l., Cagar Alam Bantimurung, 27 October 2000, M. Ôhara leg. [SU-00-MO-002] [IC-22-in05] (1 ♂ SEHU).

Diagnosis. *Atholus myrmidon* is generally identified with combinations of uninterrupted lateral stria, elytral dorsal stria complete 1–4 complete, and fine to almost no punctation of pygidium. The paramere of aedeagus is stout and is moderately broad on the medio-apical portion.

Re-description. Male. Body length: PEL: 4.00 mm; APW: 1.52 mm; PPW: 3.00 mm; EL: 2.10 mm; EW: 3.40 mm. Body (Figs 1D, 6A–C) oval with wider posterior region, convex and black; tibia, antenna, mouthparts and apical elytral margin rufous.

Head. Anterior margin of clypeus entire, anterolateral

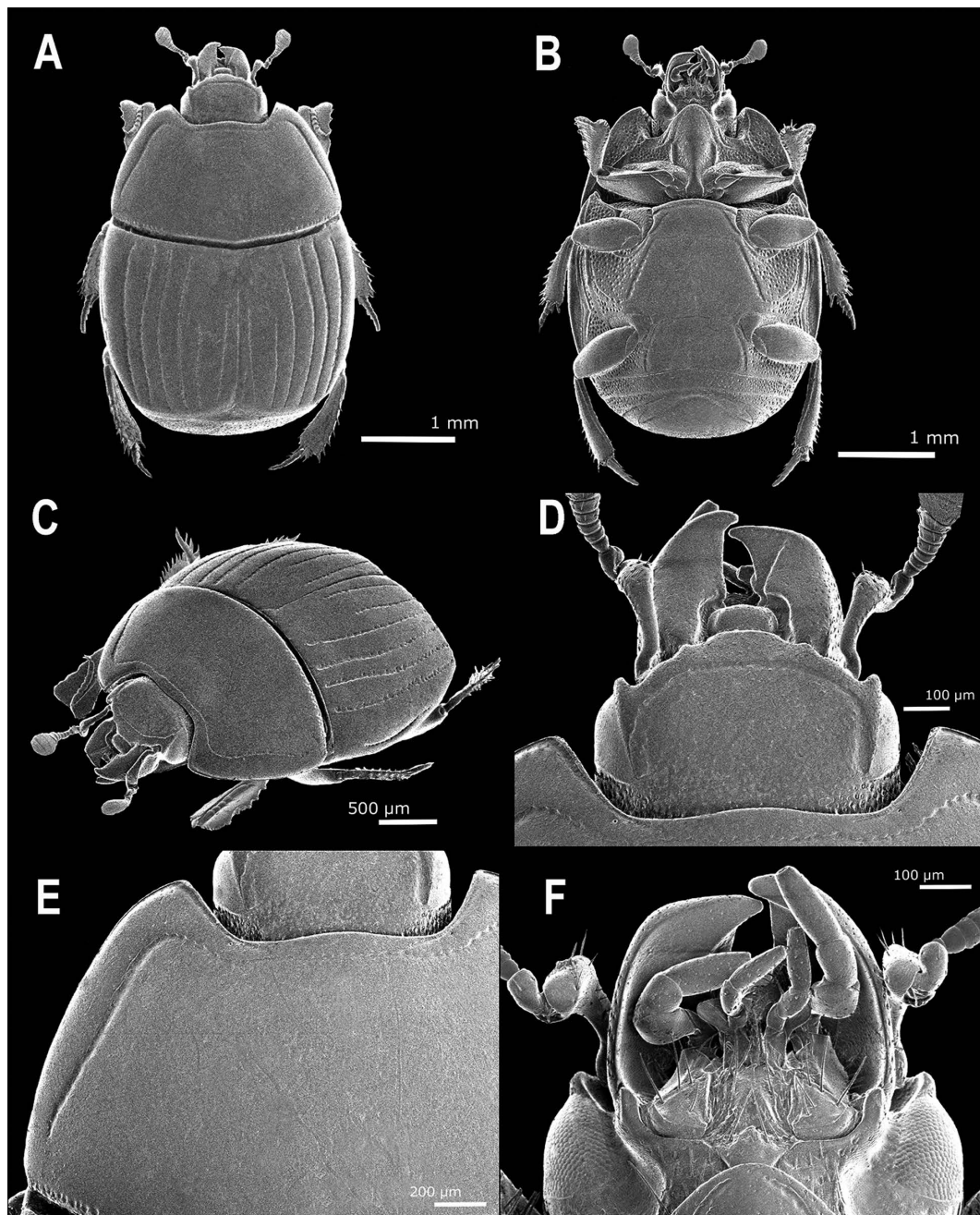


Fig. 6. *Atholus myrmidon* (Marseul, 1861), SEM micrographs, IC-22-in05. A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, dorsal view; E, pronotum; F, mouthparts, ventral view.

margin sinuous; frontal stria (Fig. 6D) round, complete and deeply impressed; disk clothed with fine punctures, which are separated by two to three times their diameter, with alutaceous ground sculpture; occipital fovea absent; eyes large and convex, well-visible dorsally; labrum finely punctated, raised and transversely long, labral fringe absent; mandible covered with fine punctations, outer margin rounded and curved inwardly, sub-apical tooth on left mandible large, mandibular apex acutely pointed.

Pronotum. Pronotum bisinuously indented and feebly narrowed on anterior portion, with angles obtuse; marginal pronotal stria laterally complete, broadly interrupted behind head; lateral pronotal stria (Fig. 6E) deeply impressed and

complete, the lateral portion rather distant from the margin, its basal end abbreviated to basal sixth of pronotal length; anterior pronotal stria present, connected to lateral stria; disk with sparse microscopic punctures, clothed with alutaceous microsculpture; area behind apical angle bare; posterior margin with row of few coarse punctures; ante-scutellar region with short, longitudinal puncture.

Elytra. Anterior margin with row of short, inconspicuous, longitudinal striae present on apical area around antero-scutellum; epipleural fossette almost no punctures on apical half; epipleural marginal stria present on apical third; elytral marginal stria complete and lightly impressed; external subhumeral stria (Fig. 7B) present medio-basally; inter-

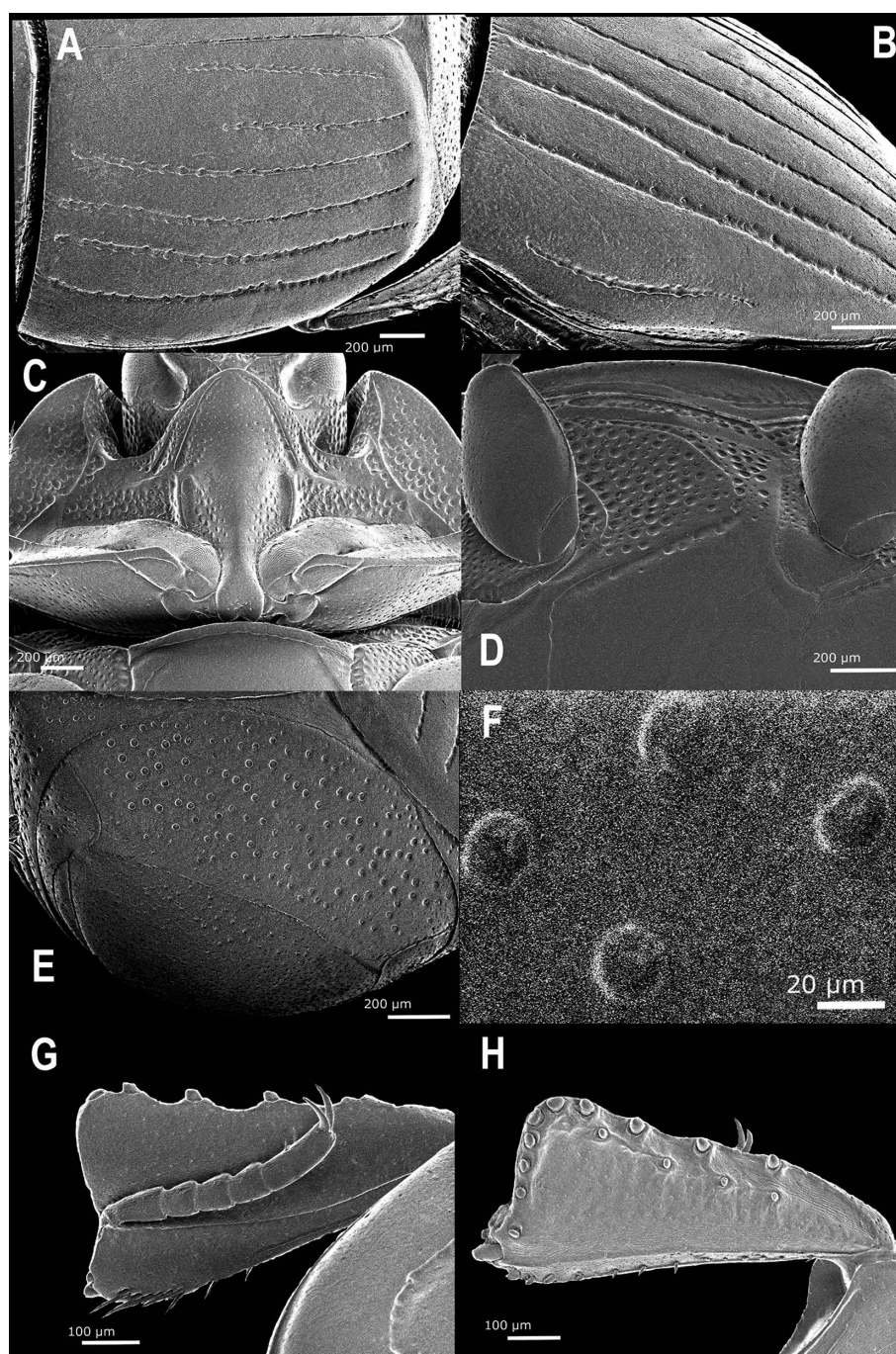


Fig. 7. *Atholus myrmidon* (Marseul, 1861), SEM micrographs, IC-22-in05. A, Elytra, dorsal view; B, ditto, oblique view; C, prosternal process; D, meso- and metaventrite; E, propygidium and pygidium; F, propygidium (punctuation); G, protibia, dorsal view; H, ditto, ventral view.

nal subhumeral stria absent; oblique stria lightly impressed on basal third; dorsal striae (Fig. 7A) 1–4 complete; dorsal 5 and sutural striae present on apical half; the sutural stria longer towards the base; disk surface similar to pronotum with alutaceous microsculpture.

Propygidium and pygidium. Propygidium (Fig. 7E, F) moderately covered with coarse and round punctures, separated by 2–5 times their diameter, the puncture about 20 µm in diameter; interspace among the coarse punctures moderately covered with fine punctations; pygidium punctations (Fig. 7E) very sparse to almost no coarse punctures, the basal half with fine and sparse punctations, becoming finer

on apex.

Prosternum. Prosternal lobe with round anterior margin (Fig. 7C), medio-apical end ascending; marginal stria deeply impressed, carinated and shortly interrupted at the middle, brief striae present on basolateral ends; lobe with moderate punctures on basolateral sides, separated by their own diameter, interspace among these punctures are sparse fine punctations, prosternal suture inconspicuous; prosternal process covered with sparse, fine punctures, the lateral sides descending; descending lateral stria deeply impressed and carinate, lateral disk with coarse punctations; basal half of process slightly narrow, posterior margin of basal lobe

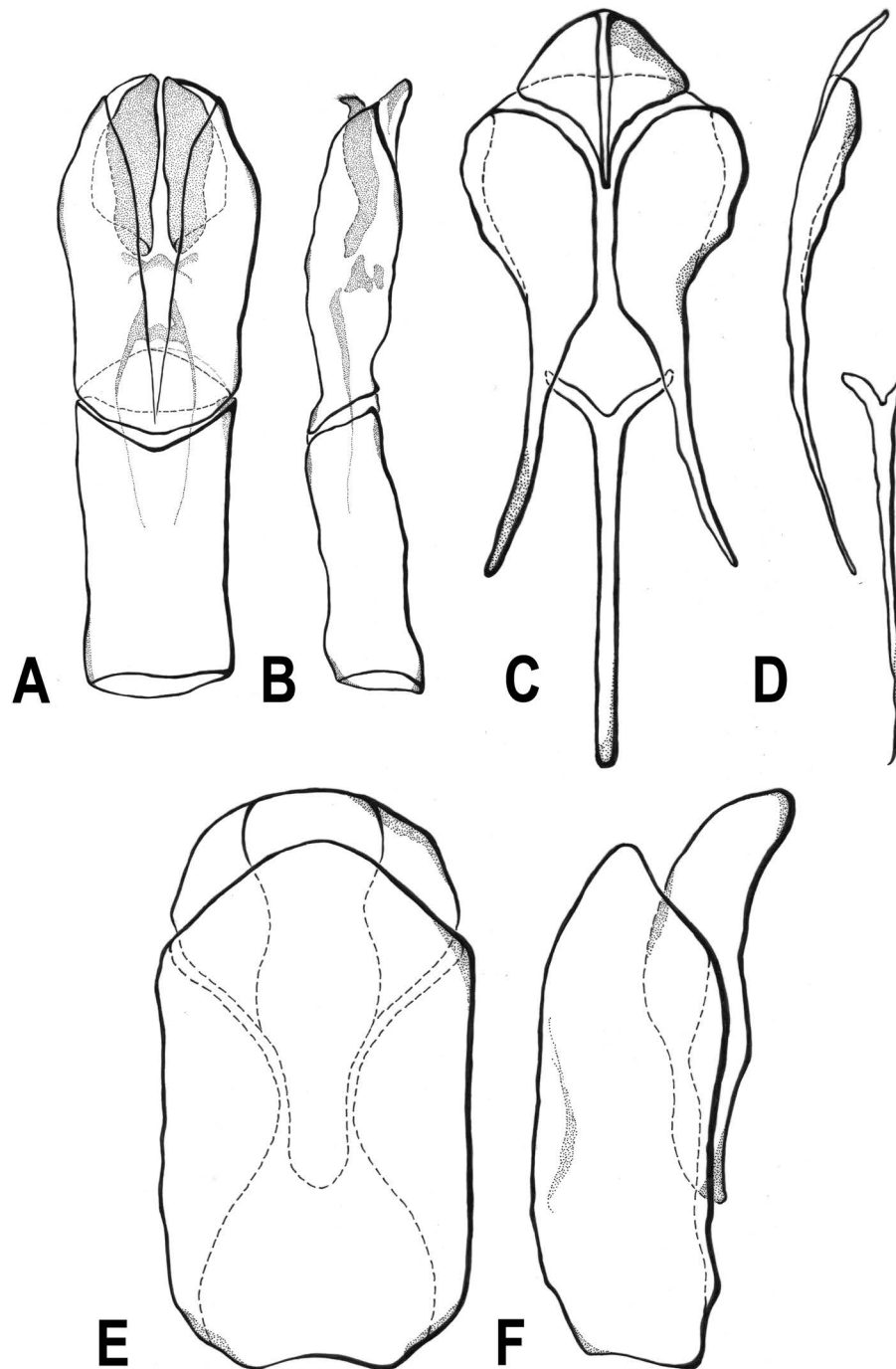


Fig. 8. *Atholus myrmidon* (Marseul, 1861), male genitalia, IC-22-in05. A, Aedeagus, dorsal view; B, ditto, lateral view; C, ninth and tenth tergites, and spiculum gastrale, dorsal view; D, ditto, lateral view; E, eighth tergite and sternite, dorsal view; F, ditto, lateral view. Scale bar: 0.20 mm.

emarginated.

Meso- and metaventrte. Anterior margin arcuate outwards (Fig. 7D), marginal stria complete and moderately impressed, stria behind anterolateral angle present; disk sparsely clothed with fine punctures, which are separated by two to three times their diameter; meso-metaventral suture lightly impressed, complete and strongly angulated at middle; lateral metaventral stria (Fig. 7D) deeply impressed and carinated, extending obliquely and posteriorly, but not united with oblique stria which extends inwardly from basal

third of metaventro-metepisternal suture; post-mesocoxal stria extending posteriorly and strongly curved along the posterior margin of mesocoxa, attaining the metaventro-mesepimeral suture; metaventrte with punctations of intercoxal disk similar to that of the apex of mesoventral plate; row of coarse punctures sometimes present along inside of basal portion of lateral stria; longitudinal suture lightly impressed; lateral disk of metaventrte densely covered with setiferous, large, round, shallow punctures; interspaces among the large punctures with sparse, fine punctations;

mesepimeron and metepimeron covered with densely setiferous, large punctures; interspaces few, fine to coarse punctations; metepisternum with very sparse punctures on apical half; first abdominal sternite with punctuation of intercoxal disk similar to that of metaventrite; surface of lateral disk similar to mesepimeron and metepimeron; lateral stria deeply impressed, slightly carinated and complete.

Legs. Anterior surface of protibia (Fig. 7G) flattened, moderately dilated and clothed with few, fine ocelloid punctures, the median area with weak strigate sculpture; outer lateral margin with three to four weak teeth topped by short denticles; anterior protibial stria complete and moderately impressed; inner marginal stria present on basal half; the inner apical margin with few sclerotized setae; posterior surface of protibia (Fig. 7H) covered with sparse, fine punctures, and strigate ground sculpture on outer basal surface, the outer region with few inconsistent ridges on surface; 10 denticles on both outer lateral margin and apical margin combined, one moderately larger on inner apical angle, 4 on outer sublateral margin; median posterior stria absent; inner posterior stria present on basal half, becoming carinate on apical half; row of sclerotized setae absent; row of setae on inner margin of protibia present on apical half, with row of setae follicles on basal half; protarsal groove shallow; profemur sparsely clothed with fine, ocelloid punctations, the surface with lightly strigate ground sculpture; marginal stria complete; anterior stria present on apical half; femoral stria almost complete; posterior margin with large and shallow punctations; row of short setae present on both basal and apical ends.

Male genitalia. Aedeagus (Fig. 8A, B) slightly stout, faintly curved ventrad on the apex; paramere about the same length as basal piece, moderately broad on medio-apical portion; median lobe moderately sclerotized, plumped on medio-apical end; eighth tergite (Fig. 8E, F) entire, with longitudinal fold on both lateral sides; ninth tergite (Fig. 8C, D) divided longitudinally, with lateral fold on both sides; tenth tergite simple. Spiculum gastrale almost as same length as ninth tergite, bifurcate on apical fifth.

Female genitalia. Not available.

Distribution. Indonesia: Greater Sunda (Sulawesi Island), New Guinea (Irian Jaya), and Laos (Fig. 12).

Remark. Only a single male specimen was available for re-examination and re-description for this species.

Atholus philippinensis (Marseul, 1854)
(Figs 1B, 11B)

Hister philippinensis Marseul, 1854: 547 (type locality: Philippines).

Hister philippensis [sic]: Gemminger and Harold 1868: 771.

Hister sectator Lewis, 1901: 375 [synonymized by Bickhardt (1917: 194)].

Atholus philippinensis: Lewis 1906: 402 (listed); Lewis 1915: 55; Mazur 1984: 215; Mazur 1997: 132; Ôhara 1999: 32–36 (Taiwan); Mazur 2011: 106 (Myanmar, Vietnam, Indonesia: Sumatra, Borneo, Java, India: Meghalaya, China: Hainan; catalogued); dela Cruz and Ôhara 2023a:

1–26 (Philippines).

Atholus sectator: Lewis 1906: 402 (listed).

Hister (Atholus) philippinensis: Bickhardt 1910: 54 (catalogued); Bickhardt 1913a: 173 (Hoozan, Taihorin); Bickhardt 1917: 194 (catalogued); Desbordes 1917: 322 (keyed); Miwa 1931: 57 (Hoozan, Taihorin); Kamiya and Takagi 1938: 31.

Specimens examined. Thirty-nine specimens of undetermined sex. **Sumatra Island:** S. Sumatra, 600 m, S. W. Lamponge, Mt. Tanggamoes, Giesting, December 1934, Lieftinck and Toxopeus leg. (1 ex. MZB). **Java Island:** Holand Indien (*Atholus philippinensis* Mars. Det. H. Desbordes, 1924), unknown collector (1 ex. MZB); Tjilatj. [= Tjilatjap], August 1925, unknown collector (4 exs MZB); Tjilatjap, Java, 10 November 1925, Drescher leg. (2 exs MZB); W. Java, Bandoeng, 17 January 1940, alt. 750 m, J. Olthof leg. (1 ex. MZB); Java, Preanger, N.O.I., Radjamandala, G. Pantjankan, 30 August 1936, alt. 400 m, F. C. Drescher leg. (1 ex. MZB); W. Java, Lembang, 18 April 1940, alt. 1200 m, J. Olthof leg. (1 ex. MZB). **Borneo Island:** West Kalimantan, Mt. Bawang, 250–300 m, October 1990, unknown collector (10 exs SEHU, 11 exs MZB); same locality, August 1990, unknown collector, (3 exs SEHU, 3 exs MZB); same locality, April 1991 [IC-22-in06], unknown collector (1 ex. SEHU).

Diagnosis. *Atholus philippinensis* can be recognized for its long and almost complete external subhumeral striae.

Distribution. India: Meghalaya, Myanmar, Vietnam, China: Hainan, Taiwan, Philippines, Indonesia: Greater Sunda (Sumatra, Java and Borneo Islands) (Fig. 11B).

Remark. Among the Indonesian *Atholus*, this species is by far the largest in size.

Atholus pinnulae (Lewis, 1900)
(Fig. 12)

Hister pinnulae Lewis, 1900: 250 (type locality: Borneo).

Atholus pennulae [sic]: Lewis 1906: 402 (listed).

Hister (Atholus) pinnulae: Bickhardt 1910: 54; Bickhardt 1917: 194 (catalogued); Desbordes 1917: 322 (keyed).

Atholus pinnulae: Mazur 1984: 215; Mazur 1997: 132; Mazur 2011: 106 (Sumatra; catalogued).

Specimens examined. No specimen available for this study.

Diagnosis. The body size of *A. pinnulae* is described as quite small, around 3.30 mm, with a hamate apical end of the lateral pronotal stria. The inner subhumeral stria is absent in *A. pinnulae* but the external subhumeral stria is impressed posteriorly. The propygidium is conspicuously punctulate, and its pygidium is smooth.

Distribution. Indonesia: Greater Sunda (Sumatra and Borneo Islands) (Fig. 12).

Atholus singalanus (Marseul, 1880)
(Figs 1F, 9A–F, 10A–H, 12)

Hister singalanus Marseul, 1880: 157 (type locality: Sumatra).

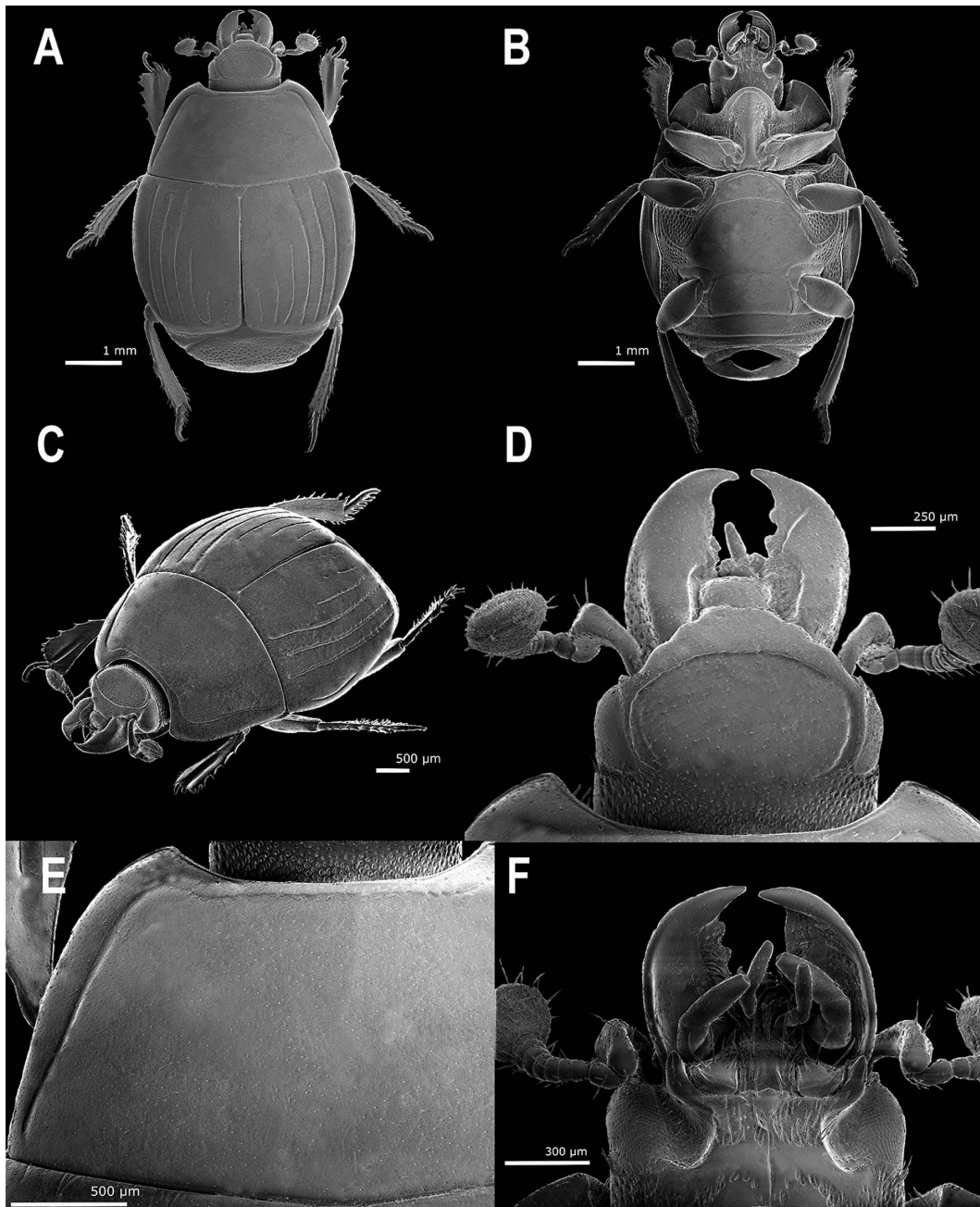


Fig. 9. *Atholus singalanus* (Marseul, 1880), SEM micrographs, IC-22-in07. A, Habitus, dorsal view; B, ditto, ventral view; C, ditto, oblique view; D, head, dorsal view; E, pronotum; F, mouthparts, ventral view.

Atholus singalanus: Lewis 1906: 402 (listed); Mazur 1984: 217; Mazur 1997: 133; Mazur 2011: 106 (catalogued).

Hister (Atholus) singalanus: Bickhardt 1910: 55; Bickhardt 1917: 194 (catalogued); Desbordes 1917: 322 (keyed).

Specimen examined. One specimen of undetermined sex. **Sumatra Island:** West Sumatra, Sukarami, Bukit Gompeng, NE 20km from Padang, 19 August 1998 [No. 9856], M. Ôhara leg. [IC-22-in07] (1 ex. SEHU).

Diagnosis. *Atholus singalanus* is generally identified for its combined character of uninterrupted lateral stria of pronotum, and very short external subhumeral stria located on the basal end.

Re-description. Body length: PEL: 3.40 mm; APW:

1.35 mm; PPW: 2.60 mm; EL: 1.85 mm; EW: 3.00 mm. Body (Figs 1F, 9A–C) oval, convex and black; tibia, antenna, mouthparts and elytral apical margin rufous.

Head. Forehead divided into two by rather weak median longitudinal impressions; anterior margin of clypeus entire and slightly produced, anterolateral margin sinuous; frontal stria (Fig. 9D) round, complete and deeply impressed; disk with alutaceous ground sculpture and clothed with very sparse, fine punctures; occipital fovea absent; eyes large and convex, well-visible dorsally; labrum punctate, raised and transversely wide, absent labral fringe; mandible covered with fine punctations, acutely pointed at apex, outer margin rounded and curved inwardly.

Pronotum. Marginal pronotal stria laterally complete and

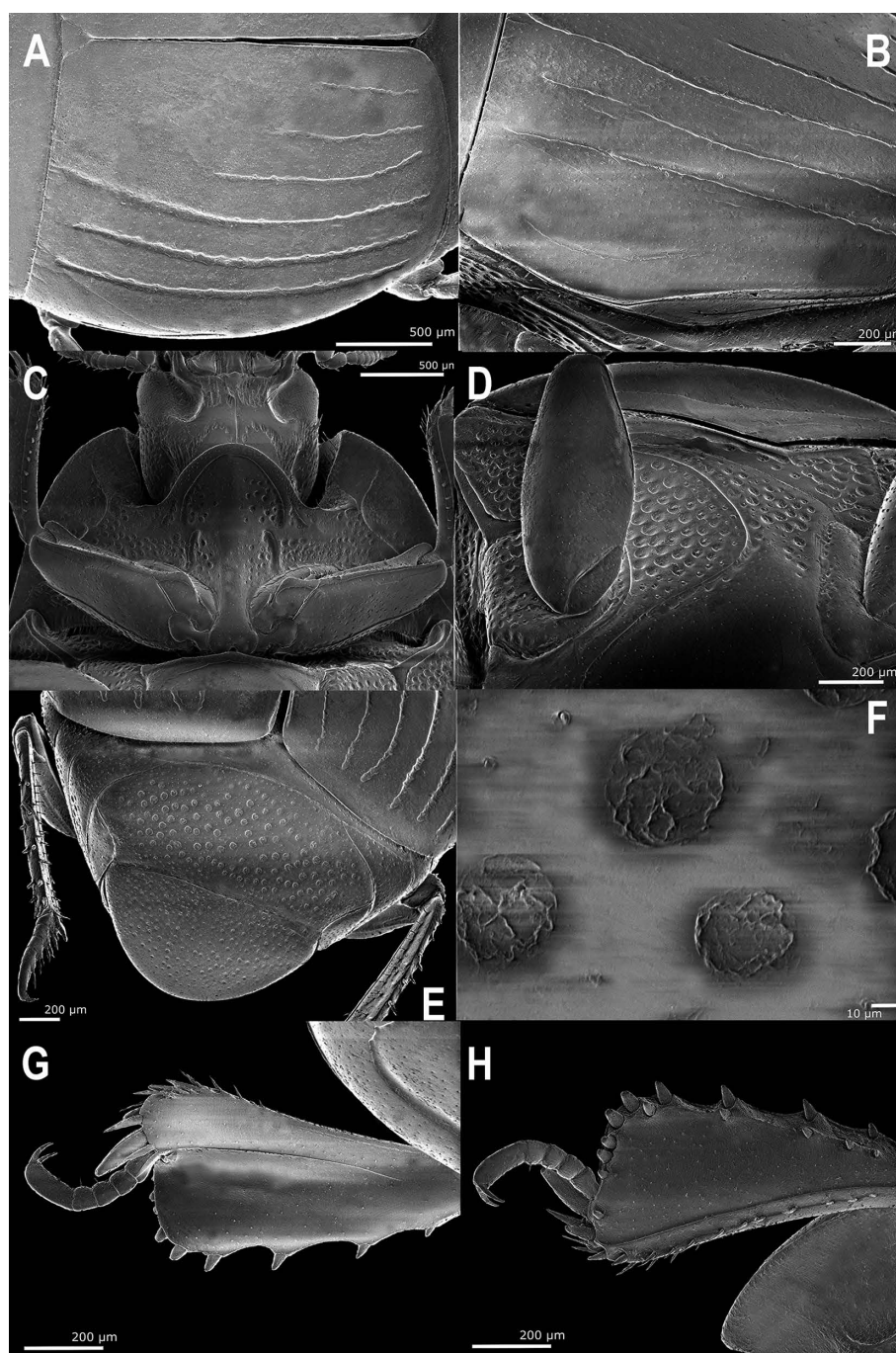


Fig. 10. *Atholus singalanus* (Marseul, 1880), SEM micrographs, IC-22-in07. A, Elytra, dorsal view; B, ditto, oblique view; C, prosternal process; D, meso- and metaventrite; E, propygidium and pygidium; F, propygidium (punctuation); G, protibia, dorsal view; H, ditto, ventral view.

broadly interrupted behind head; lateral pronotal stria (Fig. 9E) deeply impressed and complete, almost reaching the posterior margin of pronotum, lateral stria rather distant from the lateral margin; anterior pronotal stria present, connected with lateral stria; disk with sparse microscopic punctures, clothed with alutaceous microsculpture; area behind apical angle bare; posterior margin rather bare; ante-scutellar region with short, single longitudinal puncture.

Elytra. Anterior margin with short, longitudinal striae on apical area around antero-scutellum; epipleural fossette smooth and impunctate; epipleural marginal stria present on apical half; elytral marginal stria complete and moder-

ately impressed; external subhumeral stria (Fig. 10B) moderately impressed, present medio-basally and for about 1/3 of the elytral length; internal subhumeral stria absent; oblique stria slightly impressed on basal third; dorsal striae (Fig. 10A) 1–3 complete, dorsal 4 present on apical half, sometimes joined to dorsal stria 5 on apical end, dorsal stria 5 present on apical third; sutural stria shorter, present on apical fourth; discal surface similar to pronotum with alutaceous microsculpture.

Propygidium and pygidium. Propygidium (Fig. 10E, F) densely covered with coarse and round punctures, separated by their own to twice their diameter, the puncture about

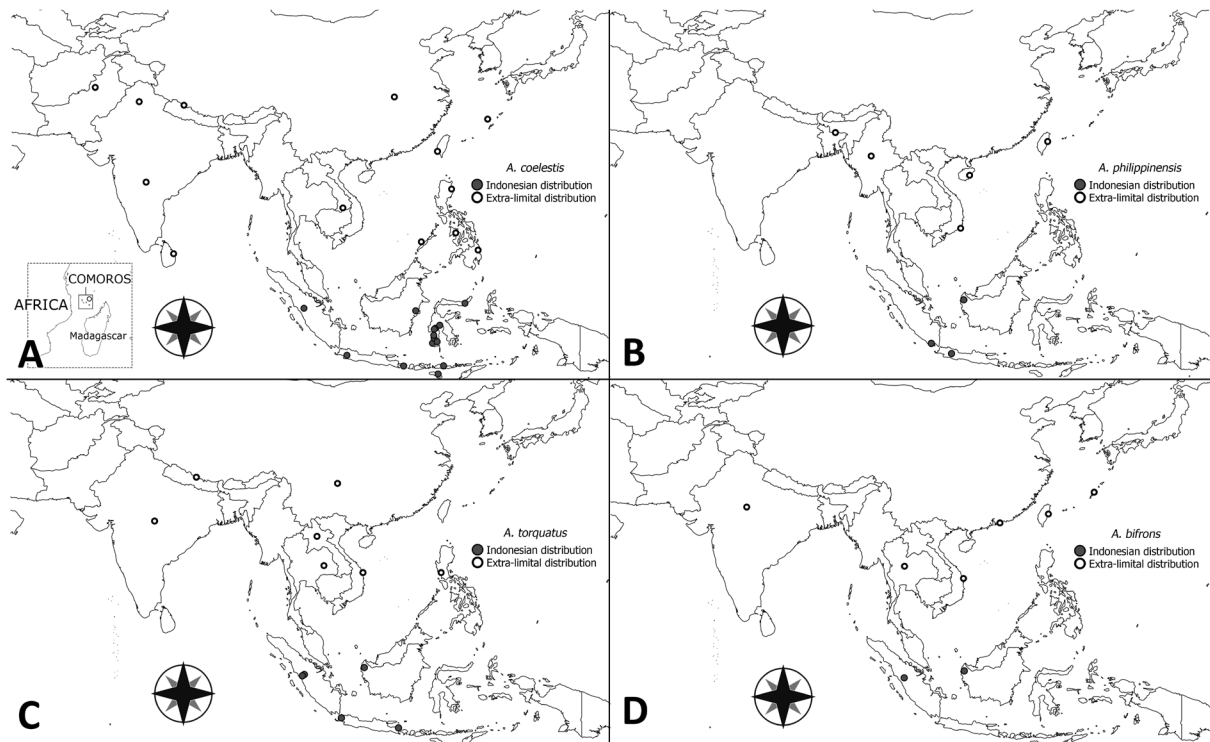


Fig. 11. Map showing the occurrence of some species of *Atholus* from the Indonesian archipelago and its extra-limital distribution in the Oriental Region. A, *Atholus coelestis*; B, *A. philippinensis*; C, *A. torquatus*; D, *A. bifrons*.

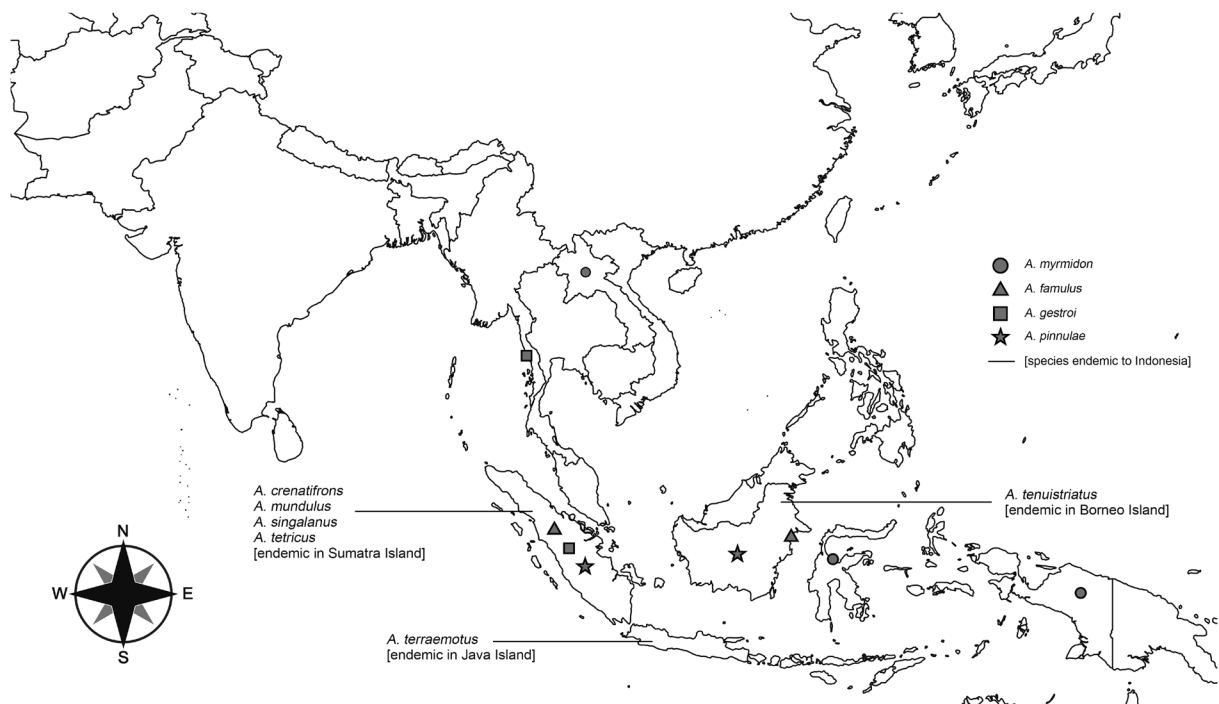


Fig. 12. Map showing the occurrence of some species of *Atholus* from the Indonesian archipelago and its extra-limital distribution in the Oriental Region.

30 μ m in diameter; interspace among the coarse punctures moderately covered with fine punctations; pygidium with punctations (Fig. 10E) similar to those of propygidium, but finer and becoming sparser on the apex, separated by their own diameter; interspace among the coarse punctures cov-

ered with fine punctations.

Prosternum. Prosternal lobe with round anterior margin (Fig. 10C), medio-apical end ascending; marginal stria deeply impressed, carinated and entire, brief striae present on basolateral ends; lobe with coarse punctures on basolat-

eral sides, the punctures separated by their own diameter, interspace among the punctures covered with sparse and fine punctations, prosternal suture inconspicuous; prosternal process covered with sparse, fine punctures, lateral sides descending; descending lateral stria deeply impressed and carinate; lateral disk with coarse punctations; basal half of process slightly narrow, posterior margin of basal lobe emarginated.

Meso- and metaventrete. Anterior margin arcuate outwards (Fig. 10D), marginal stria complete and moderately impressed, stria behind anterolateral angle present; disk sparsely clothed with fine punctures, which are separated by three to five times of their diameter; meso-metaventral suture moderately impressed, complete and carinated; metaventral lateral stria (Fig. 10D) deeply impressed, extending obliquely and posteriorly, united with oblique stria which extends inwardly from basal fifth of metaventrete-metepisternal suture, oblique stria moderately crenated; post-mesocoxal stria extending posteriorly and strongly curved along the posterior margin of mesocoxa, attaining the metaventrete-mesepimeral suture; metaventrete with punctations of intercoxal disk similar to those of mesoventral plate; row of coarse punctures sometimes present along inside of basal portion of lateral stria; longitudinal suture slightly impressed; lateral disk moderately descending medially, densely covered with setiferous, large, round and shallow punctures; interspaces among these punctures with sparse, fine to coarse punctations; mesepimeron and metepimeron covered with densely setiferous, large punctures; interspaces among the punctures with few, fine to coarse punctations; metepisternum with sparse punctures on apical half; first abdominal sternite with punctation of intercoxal disk similar to that of metaventrete; surface of lateral disk similar to mesepimeron and metepimeron; lateral stria of intercoxal disk deeply impressed, slightly carinate and complete.

Legs. Protibia (Fig. 10G) flattened on the anterior portion, slightly dilated and clothed with a few, fine ocelloid punctures; median area with weak strigate sculpture; outer lateral margin with two or three unremarkable teeth topped by short denticles; outer apical tooth weak and rounded; anterior stria moderately impressed, shortened on basal end; inner marginal stria bearing on basal half, inner apical margin with few sclerotized setae; posterior surface (Fig. 10H) covered with sparse, fine punctures, strigate ground sculpture on outer surface; outer region slightly descending; number of denticles in both outer lateral margin and apical margin combined 10, one on inner apical angle, outer sublateral margin 5; protibial spur moderately long, almost half the length of protarsus, extending from apical margin of protibia; median posterior stria complete and moderately impressed; inner posterior stria moderately impressed on basal half, with row of sclerotized setae; row of setae on inner margin of protibia with strigate ground sculpture; protarsal groove shallow; protarsus with two spine-like tarsal denticles near tarsal insertions, another one larger and more distant, located near inner anterior angle; profemur clothed with fine punctations, very few, coarse punctures on median area, surface with slightly strigate ground sculpture;

marginal stria complete, anterior stria present on apical half; femoral stria almost complete, abbreviated on basal end; posterior margin with large punctations, row of setae present on both basal and apical terminals.

Male genitalia. Not available.

Female genitalia. Not available.

Distribution. Indonesia: endemic to Sumatra Island (Fig. 12).

Remark. *Atholus singalanus* has been collected in a decaying debris of bamboo.

Atholus tenuistriatus (Lewis, 1889)
(Fig. 12)

Hister tenuistriatus Lewis, 1889: 284 (type locality: Borneo).

Atholus tenuistriatus: Lewis 1906: 402 (listed); Mazur 1984: 217; Mazur 1997: 133; Mazur 2011: 106 (catalogued).

Hister (Atholus) tenuistriatus: Bickhardt 1910: 55; Bickhardt 1917: 194 (catalogued); Desbordes 1917: 319 (keyed).

Specimens examined. No specimen available for this study.

Diagnosis. *Atholus tenuistriatus* can easily be recognized for its two pronotal lateral striae, which is a rare characteristic among the Oriental *Atholus*. Although this character-state was also recently observed in *A. lao* Mazur, 2013, the external pronotal stria in *A. tenuistriatus* is longer and almost complete compared with *A. lao*. The elytral sutural stria of this species is almost complete, while both of its propygidium and pygidium are almost impunctate, the pygidium particularly is smooth.

Distribution. Indonesia: endemic to Borneo Island (Fig. 12).

Atholus terraemotus (Lewis, 1900)
(Fig. 12)

Hister terraemotus Lewis, 1900: 248 (type locality: Java).

Atholus terraemotus: Lewis 1906: 402 (listed); Mazur 1984: 217; Mazur 1997: 133; Mazur 2011: 106 (catalogued).

Hister (Atholus) terraemotus: Bickhardt 1910: 55; Bickhardt 1917: 194 (catalogued); Desbordes 1917: 323 (keyed).

Specimens examined. No specimen available for this study.

Diagnosis. The pygidium of *A. terraemotus* is described with its densely sculptured and strigose surface. Other diagnostic characters of this species include round frontal stria anteriorly, uninterrupted lateral pronotal stria which unites anteriorly, and no subhumeral striae.

Distribution. Indonesia: endemic to Java Island (Fig. 12)

Atholus tetricus (Lewis, 1902)
(Fig. 12)

Hister tetricus Lewis, 1902: 239 (type locality: Sumatra).

Atholus tetricus: Lewis 1906: 402 (listed); Mazur 1984: 217; Mazur 1997: 133; Mazur 2011: 106 (catalogued).

Hister (Atholus) tetricus: Bickhardt 1910: 55; Bickhardt 1917: 194 (catalogued); Desbordes 1917: 321 (keyed).

Specimens examined. No specimen available for this study.

Diagnosis. *Atholus tetricus* is described with a circular fovea behind the anterolateral angle of its pronotum. The inner stria of its subhumerus is located close to apex, while its elytral dorsal striae 1–4 are complete, but the dorsal 5 and sutural stria are marked on the apical half. Both propygidium and pygidium of this species are almost impunctate, appearing smooth on their surfaces.

Distribution. Indonesia: endemic to Sumatra Island (Fig. 12).

Atholus torquatus (Marseul, 1854)
(Figs 1G, 11C)

Hister torquatus Marseul, 1854: 587 (type locality: India).

Hister genuae Lewis, 1888: 639 [synonymized by Bickhardt (1913b: 698)].

Atholus torquatus: Lewis 1906: 402 (listed); Mazur 1984: 218; Mazur 1997: 134; Mazur 2011: 106 (Nepal, Myanmar, Laos, Vietnam, Thailand, Indonesia: Java, Sumatra, China: Sichuan; catalogued); Mazur et al. 2015: 1454; dela Cruz and Ôhara 2023a: 8–16 (Philippines).

Atholus genuae: Lewis 1906: 402 (listed).

Hister (Atholus) torquatus: Bickhardt 1910: 55 (catalogued); Bickhardt 1917: 194 (catalogued); Desbordes 1917: 325 (keyed).

Hister (Atholus) genuae: Desbordes 1917: 322 (keyed).

Specimens examined. One♂, 4♀♀, 2 specimens of undetermined sex. **Sumatra Island:** West Sumatra, Bukit Gompong, Sukarami, NE 20 km from Padang, 19 August 1998, M. Ôhara leg. (1♀ SEHU); Central Sumatra, Payakumbuh, Harau Valley, November 1993, Sarimudanas leg. (1♀ MZB); Central Sumatra, Bukit Tinggi, Ngarai Sianok, 6 August 1997, T. Ito leg. (1♂ SEHU). **Java Island:** Baluran, Beokol and Banjuwangi, 16 May 1995, B. Pisarski and J. Proezyrski leg. (1♀ SEHU, 1 ex. MZB); Banten, Cidaon, Ujung Kulon, 06.4571°S, 105.1593°E, 11 March 2005, M. Ôhara leg. [JA-05-MO-013] (1♀ SEHU). **Borneo Island:** West Kalimantan, Mt. Bawang, 250–300 m, March 1990, unknown collector [IC-22-in08] (1 ex. SEHU).

Diagnosis. *Atholus torquatus* is distinguished by the combination of several characters: interrupted lateral pronotal stria, hamate on the apical end; absence of pronotal foveae near anterolateral angle and punctation on the basal half of pygidium, but becoming finer towards the apex.

Distribution. India, Nepal and China: Sichuan, Myanmar, Laos, Thailand, Vietnam, Philippines and Indonesia: Greater Sunda (Sumatra, Java and Borneo Islands) (Fig. 11C).

Remark. Two of the seven examined specimens exhibit the presence of the external subhumeral stria, an individual variability already pointed out by dela Cruz and Ôhara (2023a).

Discussion

The identity of *A. mundulus* as a valid species has been re-evaluated and reassigned as an independent species in this paper. This re-evaluation is based on a meticulous interpretation of Desbordes' remark (1919: 399) on *A. genuae*, both of which species were originally described by Lewis (1902), and Lewis (1889), respectively. Bickhardt (1914b: 314) also asserted that *Hister mundulus* is a distinct species, placing it in the subgenus *Atholus*. Desbordes clearly affirmed the subgeneric placement, although he could not identify any distinguishing characters between the two species, and drawing any conclusions proved to be challenging. The authors concur with Desbordes' suggestion of synonymy with *A. genuae*, leading us to opt not to include *A. mundulus* in the current key. However, the diagnosis of this species is still provided based on Lewis' description. Until the type specimen of *A. mundulus* can be revisited, the species should remain classified as a valid *Atholus* species.

This study re-examines seven Indonesian species of *Atholus* and provides re-description for the three Oriental species—*A. famulus*, *A. myrmidon* and *A. singalanus*—providing SEM images of their external morphology for the first time. Among the examined Indonesian species, *A. famulus* stands out as particularly peculiar, especially when compared to all the Oriental *Atholus* observed thus far. This species possesses an extremely dilated protibia that is lobe-shaped toward its anterior portion. While both the inner and outer margins of the posterior surface of protibia are also slightly broadened, appearing as trilobed, its outer sub-lateral margin does not have any denticulation. The anterior margin of its prosternum is not impressed with marginal stria, a character-state which is uncommon among Oriental *Atholus*. In addition, the basal piece of its aedeagus is longer relative the length of its parameres, which is unlike all the other *Atholus* we have examined, in which the parameres are typically longer, or at least with an equal length to its basal piece. These observations suggest that *A. famulus* may be categorized to a certain species-complex within the group. Despite these peculiarities, *A. famulus* exhibits the arcuate anterior margin of mesoventrite, along with the straight marginal stria, which are key diagnostic characters for the genus *Atholus*.

The apex of the lateral pronotal stria, commonly used to differentiate species in other *Atholus* in the Orient (dela Cruz and Ôhara 2023a; Ho et al. 2023), is also a notable characteristic observed in the examined species from Indonesia. While not all species from the archipelago are available for examination, this character is well-noted in other Indonesian *Atholus* based on their original descriptions. The lateral pronotal stria of the re-described *A. myrmidon* and *A. singalanus* is complete and continuous towards the anterior area, with an impression along the anterior margin of the pronotum, a similar observation is made in other species, such as *A. philippinensis* and *A. bifrons*. The strong and deep external stria in the subhumerus, mostly impressed on the medio-basal portion of these four species, also suggests

that these species of Oriental origin are closely related to each other. The male aedeagi of *A. philippinensis* (illustrated in Ôhara 1999), *A. bifrons* (illustrated in dela Cruz and Ôhara 2022) and *A. myrmidon* (this paper) shows similarity in general form among the species, although the male genitalia of *A. singalanus* is not available for description.

While several species of *Atholus* types were not re-visited this time, this study incorporated diagnostic characters to create a workable key for all Indonesian species to date. Most of these unexamined species exhibit interruptions in their lateral pronotal stria, either not united with the anterior stria or lacking an anterior stria altogether, as observed in *A. torquatus* and the re-described *A. famulus*. The variability in the presence of external subhumeral stria in *A. torquatus* also supports the previous inferences made by Desbordes (1917) and dela Cruz and Ôhara (2023a), suggesting a wide range of character variation among populations.

Phylogenetic relationships among Indonesian *Atholus* using morphological data sets could not be established in the present study due to the examination of only half of the known species to date, and inaccessibility of type specimens. Despite the comprehensive re-descriptions of the three re-examined species, the genitalia of the only specimen of *A. singalanus* were not found, likely detached from its body during the collection. In addition, since the single specimen of *A. myrmidon* is a male, its female genitalia remains unobserved. In most phylogenetic studies, genital structures in histerid beetles often serve as a major component for datasets (Zhou et al. 2020).

Despite these constraints, faunistic relationships among all *Atholus* species across the Indonesian archipelago can be inferred based on their current distribution. *A. coelestis* (Fig. 11A) is widely distributed and considered the most cosmopolitan species in the Indo-Malayan region. It extends towards Central Asia and the Comoros islands in the Afrotropical realm, possibly reaching further west to Europe and Continental Africa. In the Indonesian archipelago, this species occurs in all the major islands of Greater Sunda, as well as in some of the Lesser Sunda islands westward. This suggests that the species, which commonly dwells on cow and water buffalo dung, has conquered almost all islands that accommodate large ruminants. A similar distribution pattern is observed in the Philippine archipelago, where it occurs on almost all major islands (dela Cruz and Ôhara 2023a). The distributions of *A. philippinensis* (Fig. 11B), *A. torquatus* (Fig. 11C) and *A. bifrons* (Fig. 11D) also clearly indicate an Oriental range, extending from mainland Asia towards the Greater Sunda Islands of Indonesia, including the Philippines. But these species are absent in Sulawesi and the smaller islands eastward. Similarly, *A. bifrons* is currently not reported in the Philippines, despite its occurrence in Borneo, Taiwan and the recently reported from Okinawa, the Ryukyus (dela Cruz and Ôhara 2022).

On the other hand, five species of *Atholus* in Indonesia are endemic and confined to specific islands (Fig. 12), i.e., *A. crenatifrons*, *A. mundulus*, *A. singalanus* and *A. tetricus* in Sumatra, *A. tenuistriatus* in Borneo and *A. terraemotus* in Java. However, some species like *A. famulus* and *A. pinnulae*,

recorded in two islands of Greater Sunda, contribute to the overall endemism of *Atholus* in Indonesia, which is considered the highest among the areas of the Oriental region. The distribution of *A. gestroi* may also extend towards mainland Asia, as it has been reported in southern Myanmar, which is close to Sumatra. A similar case applies to *A. myrmidon*, reported in Indochina, and also extending eastward from Sulawesi Island to New Guinea.

As of now, there is no record of *Atholus* in continental Australia, suggesting that the habitat preference of *Atholus*, mostly associated with dung of large mammals originating from the mainland Asia, has not been found in Australia. The distribution patterns of a few species, such as *A. myrmidon*, extending from Laos to New Guinea, might be influenced by other factors such as oceanic and wind currents, or potentially brought about by anthropogenic movement and early domestication of ruminants among islands. Although the faunistic pattern of *Atholus* in the Indonesian archipelago is still limited due to inadequate information of how they were localized, the current distribution revealed in this study offers a glimpse into how these beetles are situated in this vast and diverse tropical region.

Acknowledgments

We would like to express our thanks to Emeritus Prof. Haruo Katakura (Hokkaido University), Emeritus Prof. Koji Nakamura (Kanazawa University), Drs. Arie Budiman and Siti Nuramaliati Prijono (LIPI = Lembaga Ilmu Pengetahuan Indonesia), for their encouragement and giving us the opportunity to study this subject and use the facilities. We also appreciate Prof. Gen Takaku (Hokkaido University of Education), Dr. Woro A. Noerdjito (MZB), Dr. Rosichon Ubaidallah (MZB) and Dr. Sih Kahono who (MZB) supported us in the field work, Ms. Maki Murakami of Hokkaido University Museum for the SEM assistance, as well as to Emeritus Prof. N. Ohbayashi (Ehime University) and Mr. Naomi Nishikawa (Sapporo) for giving us the opportunity to examine invaluable specimens. Lastly, we would also like to give thanks to Dr. Satoshi Shimano as the editor-in-charge of our manuscript, and to the reviewers, Dr. Michael Caterino and Dr. Fabio Penati, for their scrupulous and helpful insights in checking this paper.

Authors Contributions

Ian Niel dela Cruz: Conceptualization; Investigation; Formal analysis; Writing – original draft. Sri Hartini: Resources. Dhian Dwibadra: Resources; Writing – review & editing. Masahiro Ôhara: Conceptualization; Supervision; Resources; Writing – review & editing; Funding Acquisition.

Funding

This study was partly supported by KAKENHI nos

11691161 (investigator: H. Katakura) and 17405011 (M. Ôhara) from Japan Society for the Promotion of Science. The present study was carried out with the permission of LIPI as follows: in 2000 (6112/I/KS/2000), in 2003 (1148/IPH-1/KS-01/02), in 2005 (6443/SU/KS/2005), in 2006 (4744/SU/KS/2006), and in 2007 (6312/SU/KS/2007).

Declarations

Competing interests. The authors declare no conflict of interest.

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